we deduce that $\begin{pmatrix} 1 & a \\ 0 & 1 \end{pmatrix}$ belongs to the subgroup. Since $\begin{pmatrix} 1 & a \\ 0 & 1 \end{pmatrix}$ and its conjugates generate $SL_2(K)$ as a runs over all elements of K, the theorem follows.

The previous method can be used to establish the easier

THEOREM 12. Every normal subgroup of the general linear group $GL_n(K)$, which is not contained in the center, contains $SL_n(K)$, except the cases when n=2 and K has 2 or 3 elements.

- ¹ Cartan, H., Ann. école normale superieure, 64, 59-77 (1947), Theorem 4.
- ² Dieudonnè, J., Bull. Soc. math. France, 71, 27-45 (1943).
- ³ For the definition and properties of $PSL_n(K)$, see Dieudonnè.⁶
- ⁴ Dickson, L. E., Linear Groups, Leipzig, 1901.
- ⁵ Van der Waerden, B. L., Gruppen von linearen Transformationen, Berlin, 1935, p. 7.
- 6 Iwasawa, M., Proc. Imp. Acad. Japan, 17, 57 (1941).
- ⁷ The author had some difficulty in understanding Dieudonné's proof. In fact, all the parabolic elements of $PSL_2(K)$ do not form a single conjugate set in $PSL_2(K)$.

IMPRIMITIVITY FOR REPRESENTATIONS OF LOCALLY COMPACT GROUPS I

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1. Introduction.—In the classical theory of representations of finite groups by linear transformations a representation $s \to U_s$ of a finite group is said to be imprimitive if the vector space H in which the U_s act is a direct sum of independent subspaces M_1, M_2, \ldots, M_n in such a manner that each U_s transforms each M_i into some M_j . In the present note we shall discuss a generalization of this notion which is more suitable for use in connection with infinite dimensional representation because it allows the direct sum decomposition to be continuous as well as discrete. Our principal theorem (well known for finite groups) deals with weakly (and hence strongly) continuous unitary representations of separable locally compact groups. It asserts that the pair consisting of such a representation and a "transitive system of imprimitivity" for it defines an essentially unique subgroup G_0 and an essentially unique representation L of G_0 from which the original pair may be reconstructed in a quite explicit manner. This result has a number of applications. A recent theorem¹ of the author which implies the Stone-von Neumann theorem on the uniqueness of operators satisfying the Heisenberg commutation relations is included as a special case. In addition it may be used to give a complete determination of the irreducible unitary representations of the members of a class of locally compact groups which are neither compact nor Abelian.

- 2. Definition of Imprimitivity.—Let $s \to U_s$; M_1, M_2, \ldots, M_n be an imprimitive representation in the classical sense. Suppose that the U_s are unitary and that the M_t are mutually orthogonal. Let M denote the set of integers 1, 2, ..., n. For each s in the group G and each $j \in M$ let (j)s be the index of the subspace into which U_{s-1} carries M_i . Let P_i denote the projection of H on M_i . Then it is easy to see that $U_s P_i U_s^{-1} =$ More generally if P_E is defined by the equation $P_E = \sum_{(j \in E)} P_j$ for each $E \subset M$ then $U_s P_E U_s^{-1} = P_{(E)s^{-1}}$. The motivation for the following definition should now be clear. Let M be a separable locally compact space and let G be a separable locally compact group. Let x, $s \to (x)s$ denote a mapping of $M \times G$ onto M which is continuous and is such that (a) for fixed $s, x \to (x)s$ is a homeomorphism and (b) the resulting map of G into the group of homeomorphisms of M is a homomorphism. Let $P(E \to P_E)$ be a σ homomorphism of the σ Boolean algebra of all Borel subsets of M into a σ Boolean algebra of projections in a separable Hilbert space H such that P_M is the identity I. Let $U(s \to U_s)$ be a representation of G in H; that is a weakly (and hence strongly) continuous homomorphism of G into the group of unitary operators in H. If $U_s P_E U_s^{-1} = P_{(E)s^{-1}}$ for all E and s and if P_E takes on values other than O and I we shall say that U is imprimitive and that P is a system of imprimitivity for U. We shall call M the base of P. It is to be observed that P defines in M a family of null sets and that there exists in M a family of mutually equivalent measures whose sets of measure zero are precisely these null sets. The null sets are those sets E for which $P_E = 0$ and the measures are those of the form $\mu(E) = (P_E f, f)$ where f is an element in H such that $P_E f = 0$ implies $P_E = 0$.
- 3. Ergodicity and Transitivity.—When for each x and y in M there exists s in G for which (x)s = y it is natural to say that P is a transitive system of imprimitivity for U. When M is finite every system of imprimitivity decomposes in a natural manner into transitive ones corresponding to the orbits of M under G. In general, however, the decomposition of M into orbits is not reflected in a corresponding decomposition of H. It is rather the decomposition of M into ergodic or metrically transitive parts which is relevant. Accordingly we define a system of imprimitivity P to be ergodic if G acts ergodically on the base M of P; that is, whenever (E)s differs from E by a null set for all $s \in G$ then E is itself a null set or the complement of one. In view of the current literature on the decomposition of measures the study of general systems of imprimitivity may be expected to be reducible to the study of ergodic systems.

Ergodic systems which are not also transitive are rather difficult to handle and such results as we have at present are far from definitive. This note will deal exclusively with transitive systems. Fortunately in some applications it can be shown that only transitive systems can arise. Specifically let us say that the orbits of M under G are regular if there exists a countable family E_1, E_2, \ldots of Borel subsets of M, each a union of orbits such that each orbit of M is the intersection of the members of a subfamily E_{n_1}, E_{n_2}, \ldots Then the following theorem is easily proved.

THEOREM 1. If the orbits of M under G are regular then for each ergodic system of imprimitivity based on M there is an orbit C such that $P_{M-C} = 0$.

4. Formulation of the Principal Theorem.—Let P be a transitive system of imprimitivity for the representation U of the separable locally compact group G. Let x_0 be a point of the base M of P. Let G_0 be the set of all $s \in G$ for which $(x_0)s = x_0$. Then G_0 is a closed subgroup of G and the mapping $s \to (x_0)s$ of G on M defines a one-to-one Borel set preserving map of the homogeneous space G/G_0 of right G_0 cosets onto M. Thus Pis equivalent in an obvious sense to another system of imprimitivity for U whose base is the homogeneous space G/G_0 . In general we shall define a pair to be a unitary representation for the group G together with a particular system of imprimitivity for this representation. If U, P and U', P'are two pairs with the same base M we shall say that they are unitary equivalent if there exists a unitary transformation V from the space of U and P to the space of U' and P' such that $V^{-1}U_s'V = U_s$ and $V^{-1}P_E'V = P_E$ for all s and E. It follows from the above remarks that the problem of determining to within unitary equivalence all pairs based on a given M may always be reduced to the corresponding problem in which M is a homogeneous space. We shall accordingly confine ourselves to this case. The arbitrariness in the choice of x_0 has the effect only of providing us with several essentially equivalent complete systems of invariants for the pairs based on a given M.

Preparatory to stating our theorem we describe a method (which will prove to be general) of constructing pairs based on a given G/G_0 . Let μ be a finite Borel measure on G/G_0 which is "quasi invariant" in the sense that the action of G on G/G_0 preserves null sets. Let $L(\xi \to L_{\xi})$ be a representation of G_0 by unitary operators in a Hilbert space H_0 . Then let H_L be the set of all functions f from G to H_0 such that: (a) f is a Borel function in the sense that (f(s), v) is a Borel function of s for all $v \in H_0$; (b) for all $s \in G$ and all $e \leftarrow G_0$, $f(\xi s) = L_{\xi}f(s)$; and (c) (f(s), f(s)) (which by (b) is constant on the right G_0 cosets) defines a summable function on G/G_0 . By a more or less obvious adaptation of the proof of the Riesz Fischer theorem it may be shown that H_L is a Hilbert space with respect to the inner product $(f, g)_L = \int_{G/G_0} (f(s), g(s)) d\mu$ and the obvious linear operations. Naturally functions which are equal almost everywhere are to be identified. Now let ρ be the function on $G \times G/G_0$ which for each fixed s is the Radon Nikodym derivative of the translate of μ by s with

respect to μ itself. Then regarding ρ , as we may, as a function on $G \times G$ let $U_s f$ for all $s \in G$ and $f \in H_L$ be defined by the equation $(U_s f)(t) = f(ts)/\sqrt{\rho(s^-, ts)}$. It is readily verified that U_s is a unitary transformation of H_L onto itself and that the mapping $s \to U_s$ is a representation of G. For each Borel subset E of G/G_0 let ϕ be its characteristic function regarded as a function on G. For $f \in H_L$ let $(P_E f)(t) = \phi(t) f(t)$. It is easy to see that the mapping $f \to P_E f$ is a projection and that U and P together constitute a pair in the sense of the above definition. We shall call it the pair generated by L and μ . We can now formulate our main theorem.

THEOREM 2. Let G be a separable locally compact group and let G_0 be a closed subgroup of G. Let U', P' be any pair based on G/G_0 . Let μ be any quasi invariant measure in G/G_0 . Then there exists a representation L of G_0 such that U', P' is unitary equivalent to the pair generated by L and μ . If L and L' are representations of G_0 and μ and μ' are quasi invariant measures in G/G_0 then the pair generated by L' and μ' is unitary equivalent to the pair generated by L and μ if and only if L and L' are unitary equivalent representations of G_0 .

5. Outline of Proof.—We shall give the proof in outline only leaving relatively routine details to the reader. Moreover we shall assume familiarity on the part of the reader with the paper cited in reference 1 and will omit arguments similar to those given there. We shall refer to this paper as SVN. The proof falls naturally into two parts. First we show that every pair defines a representation of G_0 unique to within unitary equivalence and that two pairs defining equivalent representations of G_0 are unitary equivalent. Then we complete the proof by showing that the representation of G_0 defined by the pair generated by an arbitrary L and μ is unitary equivalent to L itself.

Given a pair U',P' based on G/G_0 we note first that the set of all $P_{E'}$ is a uniformly n dimensional Boolean algebra of projections (n = 1, 2,..., ∞) in the sense of Nakano (see SVN 5). This follows from the fairly easily proved fact that G acting on G/G_0 is ergodic. Let N denote an *n* dimensional identity representation of G_0 , let μ be a quasi invariant measure in G/G_0 and let W,P be the pair generated by N and μ . Just as in No. 6 of SVN it is possible to show that the pair U',P' is unitary equivalent to the pair U,P where P comes from the pair W,P above and U is a suitable representation of G. We define Q_s as $U_sW_s^{-1}$ and observe that $O_s P_E = P_E O_s$ for all E and s. It follows as in SVN that there exists a weakly Borel function Q^{\sim} from $G \times G$ to the group of unitary operators in the space H_1 in which the N_s act such that for each s in G we have $(Q_s f)(t) = Q^{\sim}(s, t) f(t)$. The identity $Q^{\sim}(s_1 s_2, t) = Q^{\sim}(s_1, t) Q^{\sim}(s_2, t s_1)$ holding for almost all triples is established as in SVN and from it the existence of a weakly Borel function B such that $Q^{\sim}(s, t) = B^{-1}(t)B(ts)$ almost everywhere. The fact that the functions in H_N are constant on the

right G_0 cosets implies that $Q^{\sim}(s, \xi t) = Q^{\sim}(s, t)$ for all $\xi \in G_0$ almost everywhere in s and t. This implies in turn that $B^{-1}(\xi t)B(\xi ts) = B^{-1}(t)B(ts)$ in the same sense or equivalently that $B(\xi ts)B^{-1}(ts) = B(\xi t)B^{-1}(t)$. In short for each $\xi \in G_0$, $B(\xi t)B^{-1}(t)$ is almost everywhere equal to a certain constant operator L_{ξ} . A simple argument shows that $(L_{\xi}v_0, v_1)$ is of the form $\int_{\mathcal{C}} \psi(t) (B(\xi t) v_2, v_1)$ for a dense set of v_0 's. Here v_0 , v_1 and v_2 are elements in H_1 and ψ is a continuous complex valued function vanishing outside of a compact subset of G. It follows readily that $(L_{\varepsilon}v_0, v_1)$ is continuous in ξ and, since $L_{\xi_1\xi_2} = L_{\xi_1}L_{\xi_2}$, that $L(\xi \to L_{\xi})$ is a representation of G_0 . Of course L may depend upon the choice of μ , the choice of the unitary map of the given Hilbert space on H_N and the choice of B. However, the fact that any two μ 's have the same null sets guarantees the lack of dependence of L on μ . As to the other possible dependencies note that a unitary map X of H_N on itself which commutes with all P_E is defined by an equation of the form Xf(t) = X(t)f(t) where X(t) is a unitary operator on H_1 for each t and X(t) is a weakly Borel function of t. Moreover $X(\xi t) =$ X(t) for $\xi \in G_0$. It is readily calculated that the effect on Q of a transformation by X is to replace it by R where $R(s, t) = X^{-1}(t)Q(s, t)X(ts)$. Now if $C^{-1}(t)C(ts) = X^{-1}(t)B^{-1}(t)B(ts)X(ts)$ it follows that $B(t)X(t)C^{-1}(t)$ is (modulo null sets) independent of t. Thus for some constant operator K we have C(t) = KB(t)X(t) so that $C(\xi t)C^{-1}(t) = KB(\xi t)X(\xi t)X^{-1}(t)$ $B^{-1}(t)K^{-1} = KL_{\xi}K^{-1}$. In short our original pair and in fact the unitary equivalence class to which it belongs determine L to within unitary equivalence. Conversely a simple reversal of the argument shows that pairs leading to unitary equivalent L's must be themselves unitary equivalent.

Now let L' be an arbitrary representation of G_0 and let U',P' be the pair generated by L' and a quasi invariant measure μ in G/G_0 . By the argument of the preceding paragraph there is a unitary map V^{-1} of $H_{L'}$ on some H_N such that $V^{-1}P_E'V = P_E$ where W_NP is as before the pair generated by N and μ and N is an identity representation of G_0 on a Hilbert space H_1 . It is not difficult to show that there exists a weakly Borel function V^{\sim} defined on G whose values are operators from H_1 to the space H_2 in which L' operates such that $(Vf)(t) = V^{\sim}(t)f(t)$. It follows from the fact that V is unitary that $V^{\sim}(t)$ is unitary from H_1 into H_2 for almost all t and it follows from the fact that $Vf \in H_{L'}$ that for each $\xi \in G_0$, $V^{\sim}(\xi t) =$ $L_t'V^{\sim}(t)$ for almost all t. Now the Q_s of the preceding paragraph here take the form $V^{-1}U_s'VW_s^{-1}$ so that $U_s'VW_s^{-1} = VQ_s$. Hence $V^{\sim}(ts) =$ $V^{\sim}(t)Q^{\sim}(s, t)$ or $V^{\sim}(ts) = V^{\sim}(t)B^{-1}(t)B(ts)$ or $V^{\sim}(ts)B^{-1}(ts) = V^{\sim}(t)$ $B^{-1}(t)$. Thus there exists a norm preserving operator K independent of t such that $V^{\sim}(t) = KB(t)$ for almost all t. If K were known to map H_1 onto the whole of H_2 we could write $B(t) = K^{-1}V^{\sim}(t)$ and conclude at once that $B(\xi t)B^{-1}(t)=K^{-1}L_{\xi}{'}\,V^{\sim}(t)\,V^{\sim-1}(t)K=K^{-1}L_{\xi}K$ and hence that the L for U'.P' is unitary equivalent to L'. In order to show that K is indeed

an onto mapping we must make use of certain facts about the space $H_{L'}$ which so far as we know at this point might be zero dimensional. For each continuous function w from G to H_2 which vanishes outside of a compact subset of G let \bar{w} be defined by the equation $(\bar{w}(t), v) = \int_{\sigma_0} (L_{\xi}'^{-1}w(\xi t), v)d\xi$ for all v in H_l and all t in G. This function may be shown to be a continuous member of $H_{L'}$ which vanishes outside of a set whose image in G/G_0 is compact. Arguments of a fairly routine nature show that for each $t \in G$ the vectors $\bar{w}(t)$ span H_2 . Now suppose that K does not map H_1 onto H_2 . Choose v_0 orthogonal to the range of K. Consider an arbitrary member of $H_{L'}$ of the form \bar{w} . We have $\bar{w}(t) = V^{\sim}(t)f(t)$ for some f and almost all t. But $V^{\sim}(t)f(t)$ is in the range of K for almost all t. Thus, since \bar{w} is continuous we can conclude that $(\bar{w}(t), v_0) = 0$ for all t. Hence for all t, $(\bar{w}(t), v_0) = 0$ for all \bar{w} and this contradicts the fact that the $\bar{w}(t)$ span for each t.

- 6. Reducibility.—The natural question concerning the connection between the reducibility of a pair U,P and the reducibility of the defining representation of G_0 is easily answered. If T commutes with all L_ξ then a transformation T^{\sim} taking H_N into H_N is defined by the equation $(T^{\sim}f)$ $(t) = B^{-1}(t)TB(t)f(t)$ where B is the function used in defining L. Then, as is easily seen $T \to T^{\sim}$ is a *-isomorphism of the ring of all bounded linear operators which commute with all the L_ξ onto the ring of all bounded linear operators which commute with all the U_s and all of the P_B . In particular the U_s and the P_B are simultaneously reducible if and only if L is a reducible representation of G_0 .
- 7. Application to the Determination of Group Representations.—Let G be a separable locally compact group and let G_1 be a closed normal Abelian subgroup of G. Let \hat{G}_1 denote the character group of G_1 . Every member s of G defines an automorphism $x \to sxs^{-1}$ of G_1 and this in turn induces an automorphism $y \to (y)s$ of G_1 . Now let U be any irreducible representation of G. Restricted to G_1 it admits a spectral resolution defined by a σ homomorphism P of the Borel subsets of \hat{G}_1 into a Boolean algebra of projections in the Hilbert space H in which U acts. An obvious calculation shows that $U_s P_E U_s^{-1} = P_{(E)s^{-1}}$. Thus P is a system of imprimitivity for U. Since U is irreducible P must be ergodic. If we assume that G_1 is "regularly imbedded" in G in the sense that the orbits in G_1 under G are regular then Theorem 1 tells us that G_1 may be replaced by a single orbit. Let y be a point in this orbit and let G_y be the closed subgroup of all s for which (y)s = y. Theorem 2 tells us that U is unitary equivalent to the first member of the pair generated by an irreducible representation of $G_{\mathbf{v}}$.

If G is a "semi-direct product" of G_1 and G/G_1 ; that is, if there exists a closed subgroup G_2 such that $G_1nG_2 = e$ and $G_1G_2 = G$ much more precise information is available. The reader will have no trouble in verifying the truth of

Theorem 3. Let G_1 be imbedded regularly in G and let G be a semidirect product of G_1 and G_2 . From each orbit C of G_1 under G_2 choose a member y_C . Let G_c denote the set of all $s \in G_2$ with $(y_C)s = y_C$. Then the general irreducible representation of G may be obtained as follows. Select an orbit C and an irreducible representation L of G_C . Let M be the irreducible representation of $G_1 \cdot G_C$ which coincides with L on G_C and is y_C times the identity on G_1 . Then the first member of the pair generated by M and a quasi invariant measure in $G/(G_1 \cdot G_C)$ is the required irreducible representation of G. Every irreducible representation of G may be so obtained and two such are unitary equivalent if and only if they come from the same orbit and unitary equivalent L's.

When the irreducible representations of G_2 and its subgroups are known Theorem 3 furnishes a complete description of the irreducible representations of G. This is so, in particular, when G_2 is Abelian. Moreover when G_2 is Abelian (and G_1 is imbedded regularly in G) it tells us that every irreducible representation of G is of "multiplier" form. More generally any imprimitive representation of G generated by a one-dimensional representation of a subgroup is unitary equivalent to a representation in which the underlying Hilbert space is the space of square summable functions on a homogeneous space and the action of the operator associated with G is to translate by G and multiply by a certain function (the multiplier) of G and a variable point in the homogeneous space.

When G_1 is not imbedded regularly in G Theorem 3 fails only in that it does not describe all of the irreducible representations. The ones that it does describe still exist and are irreducible. We have examples, however, showing that in general there are many others. Their existence leads to various kinds of pathological behavior which we expect to discuss at another time. Since these "extra" representations are all infinite dimensional, Theorem 3 provides an analysis of all finite dimensional representations for arbitrary semidirect products.

A number of well-known groups are regular semidirect products and Theorem 3 includes as special cases results in the literature analyzing their representations. Examples include the unique non-commutative two-parameter Lie group⁵ (a semidirect product of two lines) and the group of Euclidean motions in two space⁶ (a semidirect product of the two-dimensional translation group and the circle group). Wigner's⁶ reduction of the representation problem for the inhomogeneous Lorentz group to that for the homogeneous Lorentz group is also a consequence of Theorem 3 since the former group is a semidirect product of a translation group and the latter group.

8. Concluding Remarks.—In the mapping from a representation L of G_0 to the pair it generates one can ignore P and obtain a mapping from representations of G_0 to representations of G. It is not difficult to see that

this mapping carries the regular representation of G_0 into the regular representation of G. Thus (in view of No. 6) any analysis of the regular representation of G_0 as a direct sum or integral will define a corresponding analysis of the regular representation of G although the "parts" will not necessarily be irreducible. This decomposition when G_0 is Abelian is the subject of a recent interesting note of Godement. It was this note of Godement together with a discussion of such a space for compact groups given by A. Weil⁸ that suggested our definition of the Hilbert space H_L .

There are a number of questions suggested by the considerations of this note which we expect to investigate and report on at a later date. We close by mentioning a few of these. (1) When is the representation U of G generated by an irreducible representation L of G_0 itself irreducible? (2) When G is finite, L and U are finite dimensional and L is irreducible there is a classical theorem which says that the number of times that Ucontains a given irreducible representation V of G is equal to the number of times that the restriction of V to G_0 contains L. Weil⁸ has recently extended this theorem to compact groups. One can ask whether (and in what sense) it continues to be true for general locally compact groups. (3) To what extent is it true that an arbitrary irreducible representation of G is the imprimitive representation generated by a primitive representation L of an appropriate G_0 ? How is the possible failure of this to hold generally connected with the "extra" representations of non-regular semidirect products? (4) Theorem 2 presumably can be used to prove other theorems like Theorem 3. What are some of these? One notes in particular that G_1 can probably be replaced by any group whose representations can be decomposed into irreducible parts in a suitably manageable manner.

- * The author is a fellow of the John Simon Guggenheim Memorial Foundation on leave from Harvard University and in residence at the University of Chicago. A significant part of the work on this paper was done at each institution.
 - ¹ Mackey, G. W., Duke Math. J., 16, 313-325 (1949).
 - ² Cf. Nakano, H., Ann. Math., 42, 657-664 (1941), Hilfsatz 1.
- 3 That such a measure always exists has been indicated by Dieudonné, Ann. univ. Grenoble, NS 23, 25–53 (1948) [p. 51]. Actually one can show, and this is important for our purposes, that any two quasi invariant measures have the same null sets. These null sets are precisely the sets whose inverse images in G are null sets with respect to Haar measure.
- ⁴ In carrying through the details of this and other arguments indicated in this note it seems to be necessary to know that every Borel set in G which is a union of right G_0 cosets defines a Borel set in G/G_0 . That this is so is an easy consequence of the following two theorems in the literature. A one-to-one continuous image of a Borel subset of a complete separable metric space is a Borel set. Kuratowski, C., Topologie I, Warsaw (1933), p. 251. If g is a continuous function on a compact subset of a metric space then there exists a Borel subset on which g is one-to-one and has the same range as before. Federer, H., and Morse, A. P., Bull. Am. Math. Soc., 49, 270–277 (1943) [Theorem 5.1].

- ⁵ Gelfand, I., and Neumark, M., C. R. (Doklady), *Acad. Sci. Ukr. S. S. R.* (NS), 55, 567-570 (1947).
 - ⁶ Wigner, E., Ann. Math., 40, 149-204 (1939).
 - ⁷ Godement, R., C. R. Acad. Sci. Paris, 228, 627-628 (1949).
- ⁸ Weil, A., L'integration dans les groupes topologiques et ses applications, Paris (1940), pp. 82, 83.

LINKAGE STUDIES OF THE RAT. X

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1. Fawn Linked with Agouti in Linkage Group V.—In an earlier paper of this series, VIII, 1947, a new color gene, fawn, was described and designated by the symbol, f. Preliminary linkage tests gave only negative results, but a cross between Agouti and fawn made by Dr. King indicated possible linkage between the two genes. Additional crosses of this nature made by Castle in Berkeley fully support that hypothesis.

A non-agouti black fawn stock, aaff, was crossed with a gray race, AAFF. The F_1 animals were gray of genotype $\frac{af}{AF}$. They were back-crossed to the black fawn stock, yielding four classes of young, expected to be equal numerically, unless linkage exists between A and f. The four genotypes expected and their observed frequencies were as follows:

GRAY FAWN	BLACK FAWN	GRAY	BLACK
Aaff	aaff	<u>A a Ff</u>	aaFf
245	310	358	294

The two back-cross classes, gray fawn and black, would derive from crossover (recombination) gametes produced by the F_1 parent, whereas black fawn and gray would derive from non-crossover gametes. Clearly the non-crossovers exceed the crossovers numerically, indicating linkage.

The crossover percentage is 44.6 ± 0.97 , a highly significant statistical result.

We conclude that genes A and f lie in the same fifth chromosome of the rat. The linkage is loose but unmistakable.